Modelling the effect of temperature on the maximum growth rates of phytoplankton populations

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Abstract

Functional relationships which parameterize growth based on the Eppley temperature relationship for phytoplankton maximal growth rates are increasingly being used in marine and freshwater ecosystem models. In this paper, we demonstrate the effect of using such generalized relationships in modelling studies. Two suites of numerical experiments are carried out to investigate the sensitivity of models to generalized growth relationships. In each experiment, one hundred individual species or groups of phytoplankton are allowed to compete under a variety of growth versus temperature relationships. One suite of experiments is carried out within a simple "chemostat" type model that is forced with seasonally varying temperature and photosynthetically available radiation (PAR) fields. A second suite of experiments is carried out using a biogeochemical mixed-layer model to demonstrate the sensitivity of these models to various temperature versus growth relationships. The key difference in the biogeochemical mixed-layer simulations is in the timing of the ecosystem response to seasonal variability of the mixed-layer depth and temperature. The Eppley growth versus temperature relationship overestimates phytoplankton growth by as much as 80% during the spring when growth rates are crucial to the timing of the spring blooms. This decrease in growth rates causes a delay in the spring phytoplankton bloom which in turn results in significant changes in all other model constituents. The results from both suites of experiments show that it is important to resolve the intrinsic growth dynamics of a population in order to properly resolve the maximum growth rates of phytoplankton populations. The results also present a possible explanation for why phytoplankton are commonly found growing within water colder than their optimal temperature for growth. A dynamic growth versus temperature model is introduced that is capable of resolving the growth dynamics of

a population of phytoplankton under a variety of temperature forcing scenarios. This new growth versus temperature model/relationship will be useful in global biogeochemical models and demonstrates the importance of underlying population dynamics in controlling bulk community growth estimates.

Keywords: Phytoplankton, Temperature, Maximum Growth Rate, Population

1. Introduction

General circulation models (GCM) are currently being coupled to ecosystem models in order to simulate global ocean ecosystems. These circulation models are based on well-understood equations of motion, state, and continuity. Marine ecologists have yet to discern such relationships or "laws." The development of ecological theory with applicable equations for use in models has been slow, and the testing of these theories has been difficult due to the complex interactions between organisms and their environment.

Historically, modelling the ocean's ecosystem has been approached from an empirical perspective. Typically, ecosystem modelers develop or assemble a set of empirically-derived functions for each of the specific trophic levels and use these to control the flow of material between the model's components. These functions are then a fixed set of equations that are not allowed to acclimate to changes in the ecosystem that may arise naturally, such as changes in nutrient flux, temperature, light, species succession, competition, food availability, predation, and phenotypic, or on longer time scales, genotypic, changes. There are currently no ecosystem models that are based entirely on first principles (Behrenfeld and Falkowski, 1997a; Evans and Fasham, 1993). Models are generally based upon some level of empirical or bulk parameterizations. The task is to decide upon what level to parameterize the individual processes in order to accurately quantify the observed system response.

Microalgae are capable of carrying out photosynthesis and cellular division over a wide range of temperatures. The effects of temperature on marine algae have been studied extensively for many years (Berry and Bjorkman, 1980; Berry

and Raison, 1981; Davidson, 1991). It is well-known that phytoplankton have an optimal temperature for growth (Li, 1980). Below the optimal temperature, plant growth rates increase with temperature according to their individual Q_{10} value. The Q_{10} relationship is often parameterized using the Arrhenius function, but in a physical chemistry framework, its shape is controlled by the net effect of the Maxwell-Boltzmann relationships from all of the cellular processes which are linked to Calvin cycle enzymatic activities (Falkowski, 1980). Above the optimal temperature, growth rates decrease beyond the higher temperatures owing to inactivation or denaturation of proteins of other factors (Ratkowsky et al., 1983).

While a general shape occurs for each growth versus temperature curve, the individual shapes vary widely between different species, and even clones of the same species (Jorgensen, 1968; Falkowski, 1977; Smayda, 1969; Yoder, 1979; Suzuki and Takahashi, 1995). The reasons for this wide range in variability may not be caused solely by temperature variability but also by changes in nutrient and light conditions under which they were grown. The optimal temperature for the curves also varies with changes in the temperature at which the phytoplankton are grown (Li, 1980). However, despite differences in the shapes of the temperature versus growth curves, a general equation can be derived for maximal growth. Eppley (1972) assembled a limited data set of growth curves of phytoplankton batch cultures. From this data set, an empirical equation was derived for estimating the maximum growth rate based on temperature, $\mu_{max} = log(2)\ 0.851\ (1.066^T)$, for a given temperature T. Other growth rate versus temperature relationships have been proposed using data from other laboratory experiments (Ahlgren, 1987).

The temperature environment that a natural phytoplankton assemblage encounters is highly variable (Lande and Lewis, 1989). At the global scale, phytoplankton are exposed to temperatures ranging between -1.8 and 30 °C. In a typical

day, an individual phytoplankton cell may be exposed to a wide variety of temperature fluctuations. Unfortunately, the actual temperature fluctuations experienced by any individual phytoplankton cell are difficult to simulate using contemporary coupled circulation/ecosystem models because the actual temperature that a phytoplankton cell is exposed to is controlled by physical and biological processes which themselves have not been properly resolved in the models (i.e. circulation, vertical mixing, cell sinking rates, etc.). Furthermore, how these fluctuations actually affect the individual phytoplankton growth rates is also unknown.

The majority of ecosystem models parameterize growth with the Eppley (1972) function. The Eppley (1972) growth versus temperature relationship has been used in both cellular process models (Geider et al., 1998), global ecosystem models (Sarmiento et al., 1993; Doney et al., 1996), and bio-optical models (Moisan, 1999). The use of the Eppley (1972) growth relationship in modelling assumes that phytoplankton under optimal light and nutrient conditions will grow maximally at any temperature. Models which use this formulation for growth are unable to resolve the variability in growth rates due to species succession from changes in temperature.

The focus of this paper is to demonstrate how individual or species growth rates need to be resolved in order to accurately model net primary productivity. This paper shows that present growth versus temperature relationships do not resolve the intrinsic population dynamics that are necessary for predicting or assessing the effects of global change and other environmental perturbations on ecosystems. The model results have implications for rates of carbon flow through the ocean ecosystem—especially with regard to changes in growth rates due to absolute temperature and its variability.

2. Methods

2.1. Chemostat model

A numerical chemostat model is used for all experiments described in this section. The model is nitrogen-based and consists of a set of 100 ordinary differential equations that describe the growth of individual phytoplankton groups growing within a chemostat. The groups can be operationally defined as either individual species or phytoplankton functional groups. For the remainder of the paper we refer to them simply as groups. The general model equations can be written as:

$$\frac{dP_i}{dt} = \mu_i \, P_i \left(\frac{N}{K_N + N}\right)\left(\frac{I}{I_k + I}\right) - (r + \delta)P_i, \tag{1}$$

where μ_i is the growth rate for the ith phytoplankton group, P_i, at some given temperature, N is the nutrient concentration, which in this model is defined as NO_3, K_N and I_k are the half-saturation coefficients for the Michaelis-Menten nitrate- and light-limitation terms, respectively, r is the turnover time for the chemostat, and δ is the phytoplankton mortality rate. The turnover time, r is defined by

$$\frac{V}{F_{in}} = \frac{V}{F_{out}} = r,$$

where V is the total chemostat volume, and F_{in} and F_{out} is the fluid flow rate into and out of the vessel, respectively.

The decision to use 100 groups is not arbitrary. The model is actually a discretization of an integro-differential equation. The number of phytoplankton chosen (100) is at the lower end of the range of phytoplankton groups that is required to resolve this equation. Discretization of the integro-differential equation in effect resolves "individual" groups of phytoplankton. Configuring the model

with more than 100 phytoplankton groups does not alter the resulting net population growth rates, while the results from simulations with less than 100 groups deviate from the results obtained with higher numbers of phytoplankton.

The 100 phytoplankton equations are all coupled to an ordinary differential equation that describes the time rate of change of nitrate N as,

$$\frac{dN}{dt} = r\ (N_0 - N) - \left(\frac{N}{K_N + N}\right)\left(\frac{I}{I_k + I}\right)\sum_{i=1}^{100} \mu_i P_i, \tag{2}$$

where N_0 is the NO_3 concentration being pumped into the chemostat.

The model uses a fourth order Runga-Kutta time stepping scheme, with a 3 minute time step. For the initial conditions, the nutrient concentration is set at 0.2 mmol N m^{-3} and all phytoplankton groups are set to 0.02 mmol N m^{-3}. The Michaelis-Menton half-saturation term for the NO_3 uptake (K_N) is set to 0.5 mmol N m^{-3} and the initial slope of the primary production versus light relationship (I_k) is set to 0.025 (W $m^{-1})^{-1}$ d^{-1}. Phytoplankton specific mortality rates are set to 0.1 d^{-1}. The NO_3 concentration for the inflow N_0 is set at 2.0 mmol N m^{-3}. The chemostat's volume-specific turnover time r is set at 0.1 day^{-1}. The model simulations are run for 10 years so that the spurious solutions caused by the initial conditions in the NO_3 and phytoplankton fields are eliminated.

The model is forced using reasonable, seasonally varying temperature and light fields for a mid-latitude (32°N) ocean region (Figure 2.) The light field is simulated using a simple photosynthetically available radiance model:

$$PAR = I_0\ T_a\ \theta_z\ 0.43(1 - \alpha), \tag{3}$$

where I_0 is the solar constant (1353 W m^{-2}); T_a is the energy fraction transmitted through the atmosphere (0.8); θ_z is the solar zenith angle; and, α is the solar albedo

(0.06). The ratio of PAR to total solar energy is assumed to be 0.43, a reasonable ratio. A simple analytical model for temperature:

$$T(t) = 15 + 10\ \mathrm{COS}\left(\frac{2\pi(\mathrm{YEARDAY} - 233)}{365}\right), \tag{4}$$

causes the temperature to vary sinusoidally between 5 and 25 degrees C, a change in magnitude similar to that observed in the northwest Pacific and Atlantic regions (Oberhuber, 1988). This wide range in temperature is chosen in order to run the model to simulate ocean regions where the effects due to temperature variability would be the greatest. The subtraction of 233 to the $YEARDAY$ introduces a phase in the seasonal cycle that is typically observed in the northern midlatitude ocean region. The solar maximum occurs during the summer solstice, around 21 June, but the sea surface temperature maximum occurs some 2 months later, on 21 of August. The light and temperature fields are used solely to control the phytoplankton growth rates.

The only parameter that is changed in the simulations is the maximum specific growth rate, μ_i, all others are held constant for all phytoplankton groups. Nine separate simulations are carried out, with each simulation given a different growth versus temperature relationship. These various simulations and the differences in the growth versus temperature curves are outlined below. For brevity, these simulations will be referred to as CHEM:1, CHEM:2.1, CHEM:2.2, etc.

In CHEM:1, the maximum specific growth rate for all the phytoplankton groups is set to the maximum growth rate predicted by the Eppley (1972) equation (Figure 1A; Table 1),

$$\mu_i = log(2)\ 0.851\ (1.066^T), \tag{5}$$

where T is the temperature within the chemostat. The only modification to this equation from the original Eppley (1972) equation is the additional $log(2)$ term which converts the growth rates from doublings-per-day to d^{-1}. In this simulation,

all the individual phytoplankton groups behave similar to each other. There is no difference between any of the phytoplankton growth equations. As a result, no competition is possible between any of the phytoplankton groups. In essence, this simulation is similar to a one component phytoplankton model.

In CHEM:2.1, each individual phytoplankton group is given its own unique growth versus temperature relationship. This is done by giving each of the 100 individual phytoplankton groups a unique optimal temperature for growth. The optimal temperatures are set using a linear function of the phytoplankton group's counting index, i, where the optimal temperature,

$$T_i^{opt} = 0.5\ i,$$

such that for the 30^{th} phytoplankton group, the optimal temperature is set as 15 °C. The individual growth versus temperature curves are set using the optimal growth temperatures of each phytoplankton group and an analytical equation,

$$\mu_i = log(2)\ 0.851\ (1.066^T)\ e^{-|T-T_i^{opt}|^3/1000}. \quad (6)$$

The choice for the form of this equation is as follows. All the phytoplankton groups are allowed to have a maximal growth rate predicted by the Eppley (1972) relationship. A modified gaussian function is added which reduces the maximum growth rate predicted by the Eppley (1972) relationship at temperatures greater than T_i^{opt}. Otherwise, the model growth rates would continue to increase. Similar shaped functions have been used to parameterize individual growth rate relationships for Arctic cyanobacteria (Tang et al., 1997) and bacterial cultures (Ratkowsky et al., 1983). A plot showing the various individual specific growth rate versus temperature curves and the original Eppley (1972) growth curve is shown in Figure 3A. In these growth curves, the asymmetry in the curve is caused

solely by the increase in growth from the original Eppley (1972) phytoplankton growth versus temperature curve.

In CHEM:2.2, the unique growth versus temperature relationships are modified to make the curves more asymmetric. These growth versus temperature curves are set using an analytical equation,

$$\mu_i = \begin{cases} log(2)\ 0.851\ (1.066^T)\ e^{-|T-T_i^{opt}|^3/5000} & T \leq T_i^{opt} \\ log(2)\ 0.851\ (1.066^T)\ e^{-|T-T_i^{opt}|^3/30} & T > T_i^{opt}. \end{cases} \tag{7}$$

The individual specific growth rate versus temperature curves for CHEM:2.2 is shown in Figure 4A.

A second series of numerical experiments is carried out that is designed to investigate the model sensitivity to changes in the asymmetry of the individual growth rate versus temperature curves. Six simulations (CHEM:3.1 to CHEM:3.6) are carried out using the growth versus temperature relationship,

$$\mu_i = \begin{cases} log(2)\ 0.851\ (1.066^T)\ e^{-|T-T_i^{opt}|^3/5000} & T \leq T_i^{opt} \\ log(2)\ 0.851\ (1.066^T)\ e^{-|T-T_i^{opt}|^3/TSCALE} & T > T_i^{opt}, \end{cases} \tag{8}$$

where $TSCALE$ is decreased for each subsequent simulation, 5000, 1000, 500, 100, 10, 0, respectively. The individual specific growth rate versus temperature curves for each of these simulations is shown in Figure 5.

2.2. Biogeochemical model

A third series of numerical experiments is carried out to investigate the sensitivity of an ecosystem model to changes in the phytoplankton growth rate formulation. A modification of the nitrogen-based plankton dynamics model of Fasham et al. (1990) is used in these simulations. We refer the reader to the Fasham et al. (1990) paper for details on this model. The following modifications are made: The original Fasham et al. (1990) model used seven compartments: NO_3, NH_4, dissolved organic nitrogen, detrital nitrogen, bacteria, phytoplankton and zooplankton. The modification is made to separate the phytoplankton component

into 100 different phytoplankton groups. The modified model then became an ecosystem model composed of 106 ordinary differential equations, of which 100 are for the individual phytoplankton groups. The only difference between the phytoplankton equation in the Fasham et al. (1990) model and this model is in the maximal growth rates, V_p. Four different simulations are carried out, MIXL:1 though MIXL:4. In MIXL:1, V_p is set to a constant value of 1.538 (d^{-1}), the rate predicted by the Eppley (1972) relationship for the model simulation's mean temperature of 15 °C. In the remaining simulations, the individual growth rate versus temperature relationships are similar to those that are used in the first three chemostat simulations (ibid. Figures 1A, 3A, 4A, respectively).

The forcing used to run the simulations is similar to that used in the original Fasham et al. (1990) model. The only differences is that the incident PAR model is altered to resolve the diurnal variability and fitted to the PAR values observed in the Burmuda Atlantic Time Series (BATS; Siegel et al., 1995). These modifications are described in detail in Spitz et al. (1998). The temperature used to force the model is the same that was used in the chemostat simulations presented above. Note that these simulations should not be compared to those results presented earlier in Fasham et al. (1990) as the range in temperature that is used in this paper is not at all like that observed near Bermuda.

3. Results

3.1. Chemostat model

When growth is parameterized using the Eppley (1972) curve (CHEM:1; Figure 1A; Equation 3), NO_3 and total phytoplankton biomass vary sinusoidally with an annual periodicity (Figure 1B). The NO_3 concentration varies inversely with the total phytoplankton biomass. Because each phytoplankton group is given the same parameterization for growth, the biomass concentration of the individual phytoplankton groups covary (Figure 1C). The individual concentrations of each group are therefore, one percent of the total phytoplankton biomass concentration. As a check on the model's formulation, the biomass-specific growth rates, after accounting for the effect of nitrate- and light-limitation, are plotted against the chemostat temperature (Figure 1D). The model growth rates should and do lie on the Eppley (1972) growth rate versus temperature curve that is used to specify the individual phytoplankton growth rates.

In the CHEM:2.1 simulation, each individual phytoplankton group is given a unique growth rate versus temperature relationship which is slightly asymmetrical about its optimal temperature (Figure 3A; Equation 4). At any given temperature, only one phytoplankton group outcompetes the other groups by growing faster. The competition between individual phytoplankton groups significantly alters the time evolution of the NO_3 pool and the relative composition of the phytoplankton population (Figure 3B and 3C). Both NO_3 and total phytoplankton biomass concentrations undergo a greater variability with season than observed in CHEM:1.

Because all the phytoplankton groups in CHEM:2.1 have a unique time evolving biomass concentration (Figure 3C), a succession occurs over each seasonal cycle due to the fluctuations in forcing temperature. Unlike CHEM:1 where the

species diversity remains constant over time, the diversity in CHEM:2.1 decreases over time as the more successful phytoplankton groups outcompete the remaining groups for available NO_3. Over time, the number of phytoplankton groups with significant biomass decreases, and as a result the seasonal range of species undergoing succession also decreases. However, total dominance by one phytoplankton group does not occur even after running the simulation forward through time for 1000 years (data not shown).

While the growth rates for each of the individual phytoplankton groups are prescribed in the model equations, the average biomass-specific (community) growth rate of the entire phytoplankton pool is not. The mean biomass-specific growth rate versus temperature relationship, normalized to account for the nitrate- and light-limitation terms, is markedly different when compared to the Eppley (1972) curve (Figure 3D). The biomass-specific growth rates are significantly lower than the Eppley (1972) growth relationship during the temperature minimum and maximum. Also, the dominant phytoplankton group has an optimal temperature T_i^{opt} that is equal to the mean temperature within the chemostat. Note that in the growth equations used for both CHEM:2.1 and CHEM:2.2 (equations 4 and 5, respectively) the maximum rate of growth does not occur at the defined optimal temperature T_i^{opt} but at a higher temperature due to the increasing growth rates with temperature. Finally, it is important to note that the mean growth rate is different at any given temperature (Figure 3D) depending on whether the temperature is increasing or decreasing. The magnitude of this hysteresis is largest during the beginning of the simulation and diminishes over time as the species diversity decreases.

In the CHEM:2.2 simulation, the individual shape of the growth versus temperature relationship has a greater asymmetry about the maximal growth rate (Figure 4A), which is a more realistic rendition of the actual growth rate curves.

The resulting time evolution of both the NO_3 and the total phytoplankton biomass concentrations (Figure 4B) is relatively indistinguishable from CHEM:2.1 (c.f. Figure 3B), even though the individual phytoplankton growth versus temperature curves are different.

As in CHEM:2.1, all phytoplankton groups in CHEM:2.2 have unique time evolving biomass concentrations (Figure 4C). However, while the time evolution of the total phytoplankton biomass concentrations for CHEM:2.1 and CHEM:2.2 are very similar, the time evolution of the individual phytoplankton groups in CHEM:2.2 is not. In both CHEM:2.1 and CHEM:2.2, the phytoplankton group composition shows both a seasonal succession and a decrease in diversity through time as a result of phytoplankton competition. This decrease in diversity occurs at a faster rate in CHEM:2.2.

The mean biomass-specific growth rate versus temperature relationship, normalized to account for the nutrient- and light-limitation terms, is markedly different (Figure 4D) when compared to both CHEM:1 and CHEM:2.1 (c.f. Figures 1D and 3D) and the Eppley (1972) relationship. In CHEM:2.1, the phytoplankton grow at a rate lower than the Eppley (1972) growth curve for an equal amount of time during periods of temperature extrema. Growth rates approaching those of the Eppley (1972) curve occur only during near the average observed temperature. In CHEM:2.2, the phytoplankton spend most of the time growing at levels lower than the Eppley (1972) relationship. Growth rates approaching those of the Eppley (1972) curve occur at temperatures just below the maxima.

In CHEM:3.1 through CHEM:3.6 simulations, the individual growth rate versus temperature curves are modified in such a way as to increase the level of asymmetry in the individual growth versus temperature curves (ibid. Figure 5).

The mean biomass-specific growth rate versus temperature relationship, normalized to account for the nutrient- and light-limitation terms, differs for each case (Figure 6).

The optimal temperature T_i^{opt} required to fit the resulting population growth rates to the individual growth curve (Equation 6) increases with increasing the asymmetry of the individual growth curves, 14.5, 17.9, 19.3, 21.5, 23.25, and 25°C, for CHEM:3.1 to CHEM:3.6, respectively. Again, it is important to note that the value for T_i^{opt} does not define the temperature of maximum growth. For example, in CHEM:3.1 the T_i^{opt} required to fit the curve to the model results is 14.5°C, while the maximum growth rates occurred near 25°C. The temperature at which the phytoplankton population as a whole reaches its peak growth rate is highest for the most symmetrical (CHEM:3.1) and asymmetrical (CHEM:3.6) growth curves, with maximum growth occurring at lower temperatures for the intermediate cases (CHEM:3.2—CHEM:3.5).

3.2. Biogeochemical model

Four different parameterizations for temperature-dependent growth (Cases MIXL:1—MIXL:4) are placed into a biogeochemical model (Figure 7). These parameterizations are similar to those used in the CHEM:1—CHEM:2.3 cases, respectively. The largest differences occurrs in the timing and magnitude of the peaks in the seasonal cycles of all the model constituents. In all but the zooplankton, the springtime peak in concentrations are delayed by about one month between the two extreme simulations. An important item to note is that the zooplankton are the most sensitive to the model alterations and virtually became nonexistent. By increasing the asymmetry in the individual growth curves, the timing of the spring bloom changed, moving from late April to late May. This forced a shift in the timing of the detrital maximum (end of April to end of May);

NH_4 minimum (late April to late May); bacterial maximum (mid-April to mid-May); and, the timing (mid-April to mid-May) and magnitude (.03 to 1.3 mmol N m^{-3}) of the DON pool. The timing of the zooplankton population minimum shifted and the concentration of the zooplankton population decreased several orders of magnitude. Net primary production levels increase with increasing asymmetry to the individual growth curves. Also, the timing of the peak of the net primary production is shifted by about one month, similar to the observed shift in time of the phytoplankton biomass peak. The f-ratio or new production time series is also shifted to later in the spring and is only affected during the spring months.

4. Discussion

4.1. Temperature effects on population growth rates

Cellular process (Geider et al., 1998) and global ecosystem (Sarmiento et al., 1993; Doney et al., 1996) models often use temperature-dependent parameterizations to constrain the maximum phytoplankton growth rate. The use of such parameterizations is due in part to the accessibility of temperature data and the importance of temperature in controlling growth rate. The present temperature-dependent growth model of choice is the Eppley (1972) growth equation. In this paper, we present some of the drawbacks that arise when models do not resolve the intrinsic dynamics of a population of organisms. We have derived a function for temperature-dependent growth which is robust and incorporates dynamics which can be applied at a variety of taxonomic levels including functional group, species, and phylogenetic affinity. A comparison of the results from our new model with the Eppley (1972) formulation for growth reveals that the Eppley (1972) growth relationship overestimates growth rates at temperatures below and above a population's optimal temperature for growth. Our results can be extrapolated for use in describing and predicting growth in global ecosystem models.

We have currently parameterized the model with one hundred groups of phytoplankton which differ from each other only in their physiological growth response to temperature. The temperature-dependent response curves represent realistic growth curves for a variety of phytoplankton groups. Our model results assume that the population of phytoplankton grow with similarly shaped temperature versus growth relationships. We do not know the various temperature versus growth relationships for an assemblage of phytoplankton at any given time/temperature. However, the growth versus temperature relationships from individual isolated species, while following a general pattern, vary as widely as that used in the

model (compare Figures 1A and 3A). The model does not include any processes which would account for acclimation of the optimal temperature for growth for specific individuals. However, this time scale of acclimation competes with the time scale of succession. If the time scale for acclimation is longer than that of species succession then acclimation processes would not alter the results of this study. [Including the effect of species succession or acclimation of the optimal temperature for growth to the resulting model for growth versus temperature is discussed later.] We used realistic environmental fields to force the model. The temperature field is selected to have a large seasonal cycle so that we could test the model within widely-ranging temperature conditions.

The model also neglects potentially "hard-wired" genetic differences between various individual phytoplankton groups that might allow certain individuals to compete better under different temperatures. Such genetic variability has been reported between the "summer" and "winter" populations of the marine coastal diatom, *Skeletonema costatum*, (Gallagher, 1980). We do not include adaptation that might have arisen from genetic differences, such as temperature adaptation of RuBP carboxylase that occurs in marine Antarctic diatoms (Descolas-Gros and de Billy, 1987).

Nutrient uptake kinetics in the model are assumed to be equal for all the individual phytoplankton groups so that we focus solely on the effects of temperature on growth. However, both nutrient availability and nitrate uptake kinetics are not independent of temperature. Nitrate is generally inversely related to temperature at depths below the mixed-layer and above the subsurface nutrient maximum, and half-saturation values for Michaelis–Menten nitrate uptake kinetics increase with nitrate availability (Balch and Byrne, 1994).

Temperature effects are not solely responsible for controlling the seasonal evolution of the phytoplankton populations. Nutrients, light history, due to turbulence and seasonal changes, and other ecosystem-linked forcing such as grazing, all play prominent and dynamic roles. The science questions that were addressed in this research focussed on determining the effect of temperature on phytoplankton growth by resolving individual phytoplankton growth relationships. We are aware that in the chemostat model simulations, changes in the phytoplankton population brought about by changes in the shape of the individual growth relationships also imparted a change in time evolution of the nutrient fields which themselves were capable of affecting additional changes in the evolution of the phytoplankton populations. However, when one compares the time evolution of the nitrate fields (compare Figures 2b and 3b) within the various chemostat experiments one observes little changes in the resulting nitrate fields. The changes observed between individual chemostat experiments are primarily due to temperature effects on the phytoplankton population growth and not due to secondary effects caused by changes in the nutrient field between individual chemostat experiments.

In the biogeochemical model simulations, the model variables were significantly modified, but expected from the changes in the net phytoplankton population growth rates. It is difficult to analyze the results to quantitatively determine which process was directly responsible for the individual observed changes. For instance, did the zooplankton population decrease overall because of the decrease in food during the spring or because of the shift in food type (more phytoplankon and less bacteria). However, these changes are precipitated solely by the changes in the individual phytoplankton growth versus temperature curves.

Are the temperature-induced changes in primary production more significant than the changes that could occur due to other processes that control primary production? This depends upon what region in the ocean you look at. In coastal

regions, where shallow waters and coastal eutrophication processes create larger variability in temperature and higher levels of nutrients, the effects of temperature are significant. In oligatrophic regions, where temperature variability and nutrient concentrations are low, the effects of nutrients control would be more significant.

4.2. Effects of species succession on estimation of growth rates

A seasonal succession of phytoplankton occurred in all simulations where the individual species are given unique growth versus temperature relationships. Species succession is a natural phenomenon in the ocean but few ecosystem models address its effects on phytoplankton population growth. Succession has historically been viewed as a floristic expression that has minor effects on the community dynamics (Smayda, 1980). Multiple phytoplankton groups have been previously incorporated within ecosystem models (Moisan and Hofmann, 1996; Bissett et al., 1999) but these models have focussed on the effect that different functional groups (i.e. diatoms, dinoflagellates, cyanobacteria) have upon the ecosystem while neglecting the inherent effects caused by species succession. Species-specific models are also currently being developed for the use in remote sensing (Balch et al., 1989; Moisan and Mitchell, 1999) and remotely sensed data sets are now being used to detect individual species (Subramaniam et al., 1994 and 1999). While the application of these types of models and data sets are still in their infancy, future model development should attempt to incorporate species dynamics in order for the models to be appropriately applied at the ecosystem level.

In the model results, a "summer" population (one that is found growing in waters colder than its optimal temperature for growth) sometimes dominates while at other times a "winter" population (one that is found growing in waters warmer than its optimal temperature for growth) dominates. A hysteresis occurs in the growth rate versus temperature relationship as a result of overlapping of the

growth versus temperature relationships of the "winter" and "summer" populations (Figure 3D). The magnitude of the hysteresis varies with the asymmetries of the individual growth versus temperature relationships. As the asymmetry of the growth versus temperature relationship increases, the rate of succession increases during the "winter" to "summer" transition and decreases during the "summer" to "winter" transition, allowing the "summer" population to have a higher optimal temperature for growth and remain dominant for extended periods of the year. When the growth curves are symmetrical (i.e. CHEM:3.1), rates of succession between "winter" and "summer" populations are nearly equal and the hysteresis is more pronounced. The opposite case occurs when the growth versus temperature relationships are one-sided, with no growth at temperatures beyond the optimal temperature for growth, and a "summer" population exists throughout the year (CHEM:3.6).

Shifts between "winter" and "summer" phytoplankton populations have previously been observed in the coastal marine diatom, *Skeletonema costatum*, (Gallagher, 1980; Smayda, 1980). Additionally, Richardson et al. (2000) have concluded that temperature is the major driving force for seasonal succession between the winter diatom *Aulacoseira baicalensis* and the summer cyanobacterium *Synechocystis limnetica* in Lake Baikal. If these observed successions are caused solely by variations in temperature, the model results predict that the individual growth versus temperature relationships for each of the "winter" and "summer" populations would require symmetric shapes for those populations. For open ocean regions, where phytoplankton are typically observed growing in waters colder than their optimal temperature for growth (Li, 1980) asymmetric growth curves are expected and observed (see Figure 1). The impact of these variations on the shape of the growth curves and how they enhance the probability of success of a given phytoplankton species needs to be investigated.

4.3. Successful competition at suboptimal temperatures

In the past, researchers have attempted to predict the dominant phytoplankton group using knowledge of temperature and laboratory-derived growth relationships (Ignatiades and Smayda, 1970; Smayda, 1969). Our results show that predicting the dominant phytoplankton group requires knowledge of the mean and variance of the temperature field and the individual growth versus temperature relationships of the phytoplankton. In simulations with individual temperature-dependent growth curves, the phytoplankton group that dominates is the one that exhibits maximum growth at temperatures warmer than the mean temperature.

It has been shown for natural populations that the photosynthetic temperature optimum is higher than the temperature at which they are found (Li, 1980; Smayda, 1980) and several ideas have been postulated to explain this observation. Eppley (1972) suggested that phytoplankton do not dominate at their optimal growth temperature because the increased probability of encountering higher temperatures would, because of the abrupt decline in growth rates at supra-optimal temperatures, place them at risk or in a more suboptimal growth condition. Eppley (1972) argued that the asymmetry in the growth versus temperature relationship caused the phytoplankton to thrive within an environment colder that their optimal temperature. The results from cases with asymmetric growth curves (CHEM:3.4—CHEM:3.6) show that an increase in the asymmetry of the growth curves allows phytoplankton with higher optimal growth temperatures to outcompete those with lower optimal growth temperatures.

The temperatures of optimal growth for the dominant populations of phytoplankton are highest for the cases with the most (CHEM:3.6) asymmetric growth versus temperature curves (Figure 6). The suboptimal conditions referred to by Eppley (1972) is due to increased competition from other phytoplankton groups that grow optimally at higher temperatures. At very low levels of asymmetry

(CHEM:3.3) the temperature for optimal growth increased to that near to the most asymmetric case (CHEM:3.6). This increase is due to the general exponential increase in the maximum growth with temperature. Under symmetric growth curve conditions, phytoplankton that grow optimally at some temperature continue growing slower than phytoplankton with higher optimal temperatures for growth. Therefore, it is also possible for phytoplankton with symmetric growth curves to thrive better in waters colder than their optimal temperature for growth.

4.4. Global growth rate versus temperature relationships

The Eppley (1972) relationship gives higher estimates of phytoplankton population growth rates during certain times of the year than those from the model (Figure 6). The amount by which the Eppley curve overestimates the results depends upon the asymmetry of the individual growth versus temperature curves. The differences are greatest during the winter periods for all cases and during the summer for cases with more symmetric growth curves.

Phytoplankton isolated from the wild are commonly observed to be growing at temperatures lower than their optimum growth temperatures (Li, 1980). Growth rate versus temperature curves calculated from individual strains (Figure 1A) show that their growth rates are much less than the Eppley estimate at temperatures below their observed optimum growth temperatures (Eppley, 1972). Because the range of habitat temperatures are more or less within the range of temperatures over which the phytoplankton can grow (Suzuki and Takahashi, 1995), phytoplankton living within the colder portions of their temperature range should grow at rates lower than those predicted by the Eppley curve based upon the shapes of the individual growth versus temperature curves. Those phytoplankton that were measured to grow at rates near those predicted by the Eppley curve are likely growing at the upper end of their temperature range. This means that models which attempt to predict phytoplankton growth rates using temperature

should take into account the local range in temperature of the environment. This would allow the models to assess when the phytoplankton might be growing within suboptimal temperatures.

Recent work on developing global algorithms for use with satellite data to predict primary production estimates in the ocean has led to the creation of temperature-dependent maximum chlorophyll-specific carbon fixation relationships (Behrenfeld and Falkowski, 1997b; Balch and Byrne, 1994) that show some resemblance to the shapes of the growth versus temperature curves resulting from the model simulations presented in this paper. Balch and Byrne (1994) argue that the rapid decrease in maximum carbon assimilation at higher temperatures is due to the low concentrations of available NO_3 in the higher temperature regions. Behrenfeld and Falkowski (1997b) suggest that the decrease in maximum carbon assimilation values at high temperatures is attributed to an increase in stratification in high temperature zones which leads to nutrient-limiting conditions. Our results demonstrate that an asymmetric relationship between growth and temperature can be obtained solely from the interaction between different types of phytoplankton groups with different growth versus temperature curves. These results imply that a portion of the observed decrease in the maximum chlorophyll-specific carbon fixation rates at high temperatures may be due to temperature variability rather than nutrient limitation.

We developed a global phytoplankton population maximum growth versus temperature relationship that takes into account the mean and variability of environmental temperatures and incorporates how phytoplankton acclimate to temperature change is fit to the model results (Figure 6). This equation is written as:

$$\mu_i = \begin{cases} log(2)\ 0.851\ (1.066^T)\ e^{-|T-T^{opt}|^3/T^{low}_{scale}} & T \leq T^{opt} \\ log(2)\ 0.851\ (1.066^T)\ e^{-|T-T^{opt}|^3/T^{high}_{scale}} & T > T^{opt}, \end{cases} \tag{9}$$

where T_{scale}^{low} and T_{scale}^{high} determine the general shape or asymmetry of the growth curve, and T^{opt} is the optimal temperature for the phytoplankton population growth. In practice, this optimal growth temperature is chosen to be equal to the mean observed SST plus some fraction of the observed variance. However, it may also be estimated from data assimilation studies. The novelty of this population growth model is that it allows the growth rates to adapt to long-term population changes that may arise from climate variability while resolving the short-term fluctuations in population growth caused by local short term temperature changes.

The model depends upon some prior knowledge of the shapes of the individual growth versus temperature relationships. The utility of having such a model is that it allows for a more dynamic growth module within the ecosystem models. This is important to those models whose primary purpose is for use as a global change prediction tool.

It is also important to note that the mean and variance of the SST used should be obtained using the more appropriate Lagrangian reference frame. This is easy to do using either simulated Lagragian drifters in GCMs or for data analysis purposes from the sea surface temperature data derived from the WOCE Lagragian drifter data set (Moisan and Niiler, 1998). Because the effects over time from variations of temperature on phytoplankton population growth rates are short-lived, this mean value should be obtained by integration over a defined time period that might be set by the e-folding growth scale of the phytoplankton population.

4.5. Resolving the effects on temperature within a biogeochemical model

The biogeochemical model simulations demonstrate that these types of models are sensitive to the types of parameterizations used to estimate the maximum growth rates of phytoplankton at different temperatures. When an ecosystem model (Fasham et al., 1991) is configured to simulate an ecosystem with a temperature range of 21 to 27°C (not shown), a one week shift (later) occurs in the

timing of the spring bloom as well as large declines in the zooplankton population. Forcing with even larger temperature fluctuations (5 to 25°C) allows us to observe the potential for variability.

We found that when we used the Eppley (1972) relationship for growth, spring phytoplankton bloom inception occurred earlier in the season due to the higher growth rates than those which result from resolving the individual growth versus temperature relationships. The shift in timing of the spring bloom has already been observed in the Fasham et al. (1993) model which used the Eppley (1972) relationship within a coupled circulation/ecosystem model. A comparison of the resulting phytoplankton chlorophyll estimates produced from the Fasham et al. (1993) model for two regions showed that: (a) the spring bloom at Bermuda Station "S", a region where SST does not vary considerably, occurred about one week earlier than the actual observed spring bloom; and, (b) the spring bloom at Ocean Weather Station India, a region with a larger seasonal SST cycle, occurred about one full month earlier than the actual observed spring bloom. The results from our modelling efforts suggest that in order to correctly simulate the timing of the spring bloom the maximum growth rates for phytoplankton during late winter must be lower than that predicted by the Eppley (1972) relationship. In the Fasham et al. (1993) paper, the maximum growth rates in the region of OWS I were between 1.1 to 1.3 d^{-1}. More recent efforts to use the same ecosystem model for simulating the ecosystem at OWS I (Ryanchenko et al., 1997) reduced the maximum phytoplankton growth rate to 0.6 d^{-1} and were able to correctly simulate the timing of the spring bloom.

It is possible that the results from this study can be extrapolated to other temperature-controlled processes within the ocean ecosystem. General equations which characterize the effect of temperature on zooplankton growth (Huntley and Lopez, 1992), and bacterial growth (White et al., 1991) and have been used in

ecosystem models to assess the effects of temperature on stocks and stability of the ecosystem (Norberg and DeAngelis, 1997). These temperature relationships use assumptions similar to those used by modeling efforts that incorporate the Eppley (1972) temperature versus maximum growth relationship. However, in order to investigate the effects of temperature on other levels of the ecosystem data on species growth versus temperature relationships must first be understood.

5. Conclusions

Our results demonstrate the importance of intrinsic population variability on ecosystems. The model results show that phytoplankton population growth rates do not resemble the Eppley (1972) relationship that to date all global ecosystem models use, nor many of the other relationships presented in Behrenfeld and Falkowski (1997a) or Falkowski et al. (1998). However, the resulting population growth curves (c.f. Figure 6) are very similar in shape to the growth versus temperature relationship obtained by Behrenfeld and Falkowski (1997b) and Balch and Byrne (1994). The major differences in these curves is that the resulting growth relationship presented in this paper does not account for nutrient and light limitation. It is hoped that the results from this study will help lead to the development of better primary production models.

A new model for determining the maximum growth rate for a population of phytoplankton is presented that takes takes into account the general shape of the individual phytoplankton growth versus temperature relationships and the variability of the temperature. This new model is unique in that it is capable of resolving species succession within the global ecosystem and retains the intrinsic variability or dynamics of the population as a whole. At present, this new formulation has yet to be tested within a GCM framework. The results from the new formulation are robust when compared against simulations with 100 plus phytoplankton. Further efforts will focus on the effects of nutrient uptake variability with the hope of establishing a similar global model.

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References

Ahlgren, G., 1987. Temperature functions in biology and their application to algal growth constants. Oikos, 49: 177-190.

Balch, W.R., Eppley, R.W., Abbott, M.R. and Reid, F.M.H., 1989. Bias in satellite-derived pigment measurement due to coccolithophores and dinoflagellates. J. Plankton Res., 11: 575-581.

Balch, W.M. and Byrne, C.F., 1994. Factors affecting the estimate of primary production from space. J. Geophys. Res., 99: 7555-7570.

Behrenfeld, M.J. and Falkowski, P.G., 1997a. A consumer's guide to phytoplankton primary productivity models. Limnol. Oceanogr., 42: 1479-1491.

Behrenfeld, M.J. and Falkowski, P.G., 1997b. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr., 42: 1-20.

Berry, J.A. and Bjorkman, O., 1980. Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physiol., 31: 491-543.

Berry, J.A. and Raison, R., 1981. Responses of macrophytes to temperature. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegher (Editors), Physiological plant ecology I. Responses to the physical environment. Vol. 12A. Springer-Verlag Berlin, pp. 277-338.

Bissett, W.P; Walsh, J.J., Dieterle, D.A. and Carder, K.L., 1999. Carbon cycling in the upper waters of the Sargasso Sea: I. Numerical simulation of differential carbon and nitrogen fluxes. Deep-Sea Res. Part I, 46: 205-269.

Cloern, J.E., 1977. Effects of light and temperature on *Cryptomonas ovata* (Cryptophyceae) growth and nutrient uptake rates. J. Phycol., 13: 389-395.

Davison, I.R., 1991. Environmental effects on algal photosynthesis: Temperature. J. Phycol., 27: 2-8.

Descolas-Gros, C., and de Billy, G., 1987. Temperature adaptation of RuBP carboxylase: kinetic properties in marine Antarctic diatoms. J. Exp. Mar. Biol. Ecol., 108: 147-158.

Doney, S.C., Glover, D.M. and Najjar, R.G., 1996. A new coupled, one-dimensional biological-physical model for the upper ocean: Applications to the JGOFS Bermuda Atlantic Time-Series Study (BATS) site. Deep-Sea Res., 43: 591-624.

Durbin, E.G., 1974. Studies on the autecology of the marine diatom *Thalassiosirra nordenskioldii* Cleve. 1. The influence of daylength, light intensity, and temperature on growth. J. Phycol., 10: 220-225.

Eppley, R.W., 1963. Evaluation of certain marine algal flagellates for mass culture. Tech. Rep. No. SAM-TDR-63-91. USAF School of Aerospace Medicine. Brooks Air Force Base, Texas.

Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. Fishery Bulletin, 70: 1063-1085.

Eppley, R.W. and Sloan, R.R., 1966. Growth rates of marine phytoplankton: Correlation with light absorption by cell chlorophyll *a*. Physiol. Plant, 19: 47-59.

Evans, G.T. and Fasham, M.J.R., 1993. Themes in modeling ocean biogeochemical processes. In: G. T. Evans and M. J. R. Fasham (editors), Towards a Model of Ocean Biogeochemical Processes. NATO ASI Series Springer-Verlag Berlin, pp. 1-19.

Falkowski, P.G., 1977. The adenylate energy charge in marine phytoplankton: The effect of temperature on the physiological state of *Skeletonema costatum* (Grev.) Cleve. J. Exp. Mar. Biol. Ecol., 27: 37-45,.

Falkowski, P.G., 1980. Light-shade adaptation in marine phytoplankton. In: P. Falkowski (editor), Primary Productivity in the Sea. Plenum Press New York, pp. 99-119.

Falkowski, P.G, Behrenfeld, M.J., Esaias, W.E, Balch, W, Campbell, J.W., Iverson, R.L., Kiefer, D.A., Morel, A. and Yoder, J.A., 1998. Satellite primary productivity data and algorithm development: A science plan for mission to planet Earth. SeaWiFS Tech. Rep. Ser., Vol. 42, 36 pp.

Fasham, M.J.R., Ducklow, H.W. and McKelvie, S.M., 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. J. Mar. Res., 48: 591-639.

Fasham, M.R.J., Sarmiento, J.L., Slater, R.D., Ducklow, H.W. and Williams, R., 1993. Ecosystem behavior at Bermuda Station "S" and Ocean Weather Station "India"; a general circulation model and observational analysis. Global Biogeochem. Cycles, 70: 379-415.

Fawley, M.W., 1984. Effects of light intensity and temperature interactions on growth characteristics of *Phaeodactylum tricornutum* (Bacillariophyceae). J. Phycol., 20: 67-72.

Foy, R.H., 1983. Interactions of temperature and light on the growth rates of two planktonic *Oscillatoria* species under a short photoperiod regime. Br. Phycol. J., 18: 267-273.

Gallagher, J.C., 1980. Population genetics of *Skeletonema costatum* (Bacillariophyceae) in Narragansett Bay. J. Phycol., 16: 464-474.

Geider, R.J., MacIntyre, H.L. and Kana, T.M., 1998. A dynamic regulatory model of phytoplankton acclimation to light, nutrients, and temperature. Limnol. Oceanogr., 43: 679-694.

Guillard, R.R.L. and Ryther, J.H., 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* (Hustedt) and *Detonula confervacea* (Cleve) Gran. Can. J. Microbiol., 8: 229-239.

Hayakawa, T., Kudoh, S., Suzuki, Y. and Takahashi, M., 1994. Temperature-dependent changes in colony size of the freshwater pennate diatom *Asterionella formosa* (Bacillariophyceae) and their possible ecological implications. J. Phycol., 30: 955-964.

Huntley, M.E. and Lopez, M.D.G., 1992. Temperature-dependent production of marine copepods: A global synthesis. The American Naturalist, 140: 201-242.

Ignatiades, L. and Smayda, T.J., 1970. Autecology studies on the marine diatom *Rhizosolenia fragilissima* Bergon. I. The influence of light, temperature, and salinity. J. Phycol., 6: 332-339.

Iriarte, A. and Purdie, D.A., 1993. Photosynthesis and growth of the oceanic picoplankter *Pycnococcus provasoli* Guillard (clone Ω48-23) (Chlorophyta) to variations in irradiance, photoperiod and temperature. J. Exp. Mar. Biol. Ecol., 168: 239-257.

Jorgensen, E.G., 1968. The adaptation of planktonic algae II. Aspects of the temperature adaptation of *Skeletonema costatum.* Physiologia Plantarum, 21: 423-427.

Lande, R. and Lewis, M.R., 1989. Models of photoadaptation and photosynthesis by algal cells in a turbulent mixed layer. Deep-Sea Res., 8: 1161-1175.

Li, W.K.W., 1980. Temperature adaptation in phytoplankton: Cellular and photosynthetic characteristics. In: P. Falkowski (editor), Primary Productivity in the Sea. Plenum Press New York. pp. 259-279.

Li, W. K. and Morris, I., 1982. Temperature adaptations in *Phaeodactylum tricornutum* Bohlin: Photosynthetic rate compensation and capacity. J. Exp. Mar. Biol. Ecol., 58: 135-150.

Maddux, W.S. and Jones, R.F., 1964. Some interactions of temperature, light intensity, and nutrient concentration during the continuous culture of *Nitzchia closterium* and *Tetraselmis* sp. Limnol. Oceanogr., 9: 79-86.

Miller, R.L. and Kamykowski, D.L., 1986. Effects of temperature, salinity, irradiance and diurnal periodicity on growth and photosynthesis in the diatom *Nitzschia americana*: Light-saturated growth. J. Phycol., 22: 339-348.

Moisan, J.R. and Hofmann, E.E., 1996. Modeling Nutrient and Plankton Processes in the California Coastal Transition Zone 1. A Time- and Depth-Dependent Model. J. Geophys. Res., 101: 22,647-22,676.

Moisan, J.R. and Niiler, P.P., 1998. Biogeochemical response to mesoscale physical forcing in the North Pacific. Western Geophysical Meeting Taipea Tiawan July 21-24.

Moisan, T.A. and Mitchell, B.G., 1999. Photophysiological acclimation of *Phaeocystis antarctica* Karsten under PAR Light Limitation. Limnol. Oceanogr., 44: 247-258.

Norberg, J. and DeAngelis, D., 1997. Temperature effects on stocks and stability of a phytoplankton-zooplankton model and the dependence on light and nutrients. Ecological Modelling, 95: 75-86.

Oberhuber, J.M., 1988. An atlas based on the 'COADS' data set: The budgets of heat, buoyancy and turbulent kinetic energy at the surface of the global ocean. Max-Planck-Institute for Meteorology, Report No. 15, 20 pp.

Paasche, E., 1968. Marine plankton algae grown with light-dark cycles. II. *Ditylum brightwellii* and *Nitzschia turgidula.* Physiol. Plant, 21: 66-77.

Ratkowsky, D.A., Lowry, R.K., McMeekin, T.A., Stokes, A.N. and Chandler, R.E., 1983. Model for bacterial culture growth rate throughout the entire biokinetic temperature range. J. of Bacteriology, 154, 1222-1226.

Richardson, T.L., Gibson, C.E. and Heaney, S.I., 2000. Temperature, growth and seasonal succession of phytoplankton in Lake Baikal, Siberia. Freshwater Biology, 44: 431-440.

Ryabchenko, V.A., Fasham, M.J.R., Kagan, B.A. and Popova, E.E., 1997. What causes short-term oscillations in ecosystem models of the ocean mixed layer? J. Mar. Sys., 13: 33-50.

Sarmiento, J.L., Slater, R.D., Fasham, M.J.R., Ducklow, H.W., Toggweiler, J.R. and Evans, G.T., 1993. A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. Global Biogeochemical Cycles, 7: 417-450.

Siegel, D.A., Michaels, A.F., Sorensen, J.C., O'Brien, M.C. and Hammer, M.A., 1995. Seasonal variability of light availability and utilization in the Sargasso Sea. J. Geophys. Res., 100: 8695-8713.

Smayda, T.J., 1969. Experimental observations on the influence of temperature, light, and salinity on cell division of the marine diatom, *Detonula confervacea* (Cleve) Gran. J. Phycol., 5: 150-157.

Smayda, T.J., 1980. Phytoplankton species succession, In: I. Morris (editor), The Physiological Ecology of Phytoplankton. University of California Press Berkeley California, pp. 493-570.

Smith, R.E.H., Stapleford, L.C. and Ridings, R.S., 1994. The acclimated response of growth, photosynthesis, composition, and carbon balance to temperature in the psychrophilic ice diatom *Nitzschia seriata.* J. Phycol., 30: 8-16.

Sorokin, C. and Krauss, R.W., 1958. The effects of light intensity on the growth rates of green algae. Plant Physiol., 33: 109-113.

Sorokin, C. and Krauss, R.W., 1962. Effects of temperature & illuminance on Chlorella growth uncoupled from cell division. Plant Physiol., 37: 37-42.

Spitz, Y. H., Moisan, J.R., Abbott, M.R. and Richman, J.G., 1998. Data assimilation and a pelagic ecosystem model: Parameterization using time series observations. Journal of Marine Systems, 16: 51-68.

Subramaniam, A. and Carpenter, E.J., 1994. An empirically derived protocol for the detection of blooms of the marine cynabocterium Trichodesmium using CZCS imagery. Int. J. Rem. Sens., 15: 1559-1569.

Subramaniam, A., Carpenter, C., Karentz, D. and Falkowski, P., 1999. Bio-optical properties of the marine diazotrophic cyanobacteria *Trichodesmium* spp. I. Absorption and photosynthetic action spectra. Limnol. Oceanogr., 44: 608-617.

Suzuki, Y. and Takahashi, M., 1995. Growth responses of several diatom species isolated from various environments to temperature. J. Phycol., 31: 880-888.

Tang, E.P.Y., Tremblay, R. and Vincent, W.F., 1997. Cyanobacteria dominace of polar freshwater ecosystems: Are high-latitude mat-formers adapted to low temperature? J. Phycology, 33: 171-181.

Thompson, P.A., Guo, M., Harrison, P.J. and Whyte, J.N.C., 1992. Effects of variation in temperature, I On the biochemical composition of eight species of marine phytoplankton. J. Phycol., 28: 481-488.

Verity, P.G., 1982. Effects of temperature, irradiance, and daylength on the marine diatom *Leptocylindrus danicus* Cleve. IV. Growth. J. Exp. Mar. Biol. Ecol., 60: 209-222.

White, P.A., Kalff, J., Rasmussen, J.B. and Gasol, J.M., 1991. The effects of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitiats. Microb. Ecol., 21: 99-118.

Yoder, J.A., 1979. Effect of temperature on light-limited growth and chemical composition of *Skeletonema costatum* (Bacillariophyceae). J. Phycol., 15: 362-370.

Table 1. values of parameters used to define the growth versus temperature relationships used in the various numerical experiments.

Case	Type	Growth Relationship	Curve Symmetry $T_{scale}^{low} :: T_{scale}^{high}$
CHEM:1	Chemostat	Eppley Relationship*	NA
CHEM:2.1	Chemostat	Individual Growth Curves†	1000:1000
CHEM:2.2	Chemostat	Individual Growth Curves	5000:30
CHEM:3.1	Chemostat	Individual Growth Curves	5000:5000
CHEM:3.2	Chemostat	Individual Growth Curves	5000:1000
CHEM:3.3	Chemostat	Individual Growth Curves	5000:500
CHEM:3.4	Chemostat	Individual Growth Curves	5000:100
CHEM:3.5	Chemostat	Individual Growth Curves	5000:10
CHEM:3.6	Chemostat	Individual Growth Curves	5000:0
MIXL:1	Mixed-Layer	Constant Value‡	NA
MIXL:2	Mixed-Layer	Eppley Relationship	NA
MIXL:3	Mixed-Layer	Individual Growth Curves	1000:1000
MIXL:4	Mixed-Layer	Individual Growth Curves	5000:30

* Eppley temperature versus growth relationship.

† Individual growth versus temperature relationships used; ratios reflect the exponential decay scale of the curves about the optimal growth temperature

‡ mean growth rate for 15°C using the Eppley relationship

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Fig. 1. Results from the CHEM:1 simulation in which all individual phytoplankton groups are given a growth versus temperature relationship that was equal to the (**A**) maximum specific growth versus temperature relationship from Eppley (1972; thick solid curve). For comparison, the actual measured specific growth rate (d^{-1}) versus temperature curves obtained from various laboratory experiments (solid curves) are shown. Data are from Suzuki and Takashi (1995), Smayda (1969), Guillard and Ryther (1962), Sorokin and Krauss (1958, 1962), Eppley (1963), Eppley and Sloan (1966), Paasche (1968), Moisan (1999), Cloern (1977), Maddux and Jones (1964), Jorgensen (1968), Yoder (1979), Hayakawa et al. (1994), Miller and Kamykowski (1986), Smith et al. (1994), Durbin (1974), Ignatindes and Smayda (1970), Foy (1983), Thompson et al. (1992), Smayda (1979), Fawley (1984), Falkowski (1977), Li and Morris (1982), Verity (1982), and Iriarte and Purdie (1993). The resulting total phytoplankton (**B** solid curve) and NO_3 (**B** dashed curve) concentrations, and the individual phytoplankton (**C**) concentrations reflect typical chemostat behavior. The individual phytoplankton concentration in this case are all equal to each other since their growth rate versus temperature relationships did not differ, hence only one curve is observed. The population growth rates (**D**, thick curve) are shown in comparison with the growth versus temperature relationship from Eppley (1972, thin solid curve).

Fig. 2. Time series of the seasonally varying (**A**) temperature (°C) used to force the chemostat simulations (dashed curve) and the biogeochemical model simulations (both dashed and solid curved), and (**B**) photosynthetically available radiance (PAR; W m^{-2}) used to force all of the simulations.

Fig. 3. Composite plot **A**) of the 100 individual specific growth versus temperature relationships (solid curves) for the CHEM:2.1 chemostat simulation. Five of the possible 100 individual curves are shown so that the shapes of individual curves can be discerned from one another. The maximum specific growth versus temperature relationship from Eppley (1972; dashed curve) is shown for comparison and demarcates the maximum range allowed by each of the individual growth versus temperature curves. The resulting total phytoplankton (**B** solid curve) and NO_3 (**B** dashed curve) concentrations show a steady-state seasonal cycle, while individual phytoplankton concentrations (**C**, overlapping curves)) do not reach a steady-state. The population growth rates (**D**, thick curve) are shown in comparison with the growth versus temperature relationship from Eppley (1972, thin solid curve) and a curve fit through the resulting population growth rates (thick dashed curve).

Fig. 4. Same as for Figure 4, but for the CHEM:2.2 simulation.

Fig. 5. Series of 6 (**A** through **F**) different composite plots of the 100 individual specific growth versus temperature relationships (solid curves) used in a growth curve sensitivity simulations. Five of the possible 100 individual curves are shown so that the shapes of individual curves can be discerned from one another. The asymmetry (steepness) of the curves increases from **A** through **F**.

Fig. 6. The resulting population growth rates resulting from the sensitivity simulations in which the individual specific growth versus temperature relationships are shown in Figure 6. The population growth rates (thick curve) are shown in comparison with the growth versus temperature relationship from Eppley (1972, thin solid curve) and a curve fit through the resulting population growth rates (thick dashed curve).

Fig. 7. Time evolution of the **A** mixed-layer depth, **B** NO_3, **C** NH_4, **D** dissolved organic nitrogen, **E** detritus, **F** bacteria, **G** total phytoplankton, **H** zooplankton, **I**

net primary production, and **J** f-ratio for MIXL:1—MIXL:4 (solid, small, medium and large dashed curves, respectively) of the biogeochemical model simulations.